

**Distribution, life history and conservation assessment of the
critically endangered butterfly *Pseudolucia parana*
(Lepidoptera: Lycaenidae)**

Dubi BENYAMINI^{1*}, Nicolás Oliveira MEGA², Helena Piccoli ROMANOWSKI², Alfred MOSER³,
Roger VILA⁴ & Zsolt BÁLINT⁵

¹ 4D MicroRobotics Ltd., 91 Levona Str., Beit Arye, 7194700 Israel.

E-mail: dubi_ben@netvision.net.il

² Laboratório de Ecologia de Insetos, Depto. Zoologia, PPG Biologia Animal, Instituto de
Bióciências. UFRGS – Universidade Federal do Rio Grande do Sul, Porto Alegre, 43435, Brasil.

E-mails: hpromano@ufrgs.br, nicolas.mega@gmail.com

³ Av. Wilhelm Rotermond, 1045-São Leopoldo, RS, Brasil. E-mail: a.moser@ensinger.com.br

⁴ Institut de Biologia Evolutiva (CSIC-Universitat Pompeu Fabra),

Passeig Marítim de la Barceloneta 37, 08003 Barcelona, Spain. E-mail: roger.vila@scic.es

⁵ Hungarian Natural History Museum, Department of Zoology,

H-1088 Budapest, Baross utca 13, Hungary. E-mail: balint.zsolt@nhmus.hu

Abstract – *Pseudolucia parana* Bálint, 1993 was described from Castro, Paraná, Brazil, where it was first collected over 120 years ago. It was observed/collected quite sporadically in the second half of the 20th century in a few isolated habitats in the State of Paraná. Excluding a single record since the early 2000s, the species was not observed in all its known sites in Paraná due to urbanization of its habitats or change of land use. Consequently the species in Paraná state is highly endangered, possibly extinct. Efforts to find the species in the state Santa Catarina failed. A new hope to the survival of the species appeared in the southernmost state Rio Grande do Sul, where some relict populations are documented. The results of rescue expeditions to several granitic hills in the region are presented and the current distribution *P. parana* is assessed. First descriptions of its early stages, ecology, ethology and recommendations for conservation are given. The data provided indicate that the global status of *P. parana* should be Critically Endangered. Some molecular traits of *P. parana* are analysed resulting in a preliminary assessment for the age of the populations. With 24 figures.

Key words – Brazil, campos sulinos, early stages, Paraná, relict, Rio Grande do Sul, south Brazilian grasslands

* Corresponding author.

INTRODUCTION

Brazil is known for its high degree of endemism. In all its regions attractive and rare taxa of butterflies occur, ideal candidates for flagship species for nature protection activities. A good example is the spectacular nymphalid *Morpho aega* (Hübner, 1822), an endemic species of the Atlantic Forest region. Even the relatively less known family Lycaenidae, represented by two tribes in the Atlantic Forest, offers several species for conservation interests, for example the gorgeous endemic *Arcas ducalis* (Westwood, 1852), the Ducal Arcas (BROWN 1993a). This species belongs to the tribe Eumaeini, which contributes 95% of Neotropical lycaenid diversity both in species and genera richness (BROWN 1993b, ROBBINS 2004). The number of species of the other tribe, Polyommataini, is extremely low and contains species that rarely attract the interest of non-specialists. In spite of being small and cryptic in pattern and colouration, the study of some key species may help understanding and protect unique threatened ecosystems in the Atlantic Forest.

However, in spite of the fact that the Neotropical region is almost always remembered due to its forested environments, it contains extremely rich non-forested ecosystems that cover almost a third of its area. For example, grasslands are dominant at the southern tip of Brazil, yet areas with well-preserved pristine native fields and vegetation are scarce and diminishing over the years. These remnants are distributed in mosaics in the Atlantic Forest (from Paraná to the Brazilian Southern Plateau of Rio Grande do Sul) and in the Pampa biome (Rio Grande do Sul) and may be called “Campos Sulinos” (ANDRADE *et al.* 2019). Grassland areas are among the most species-rich ecosystems (WILSON *et al.* 2012), but are still only very poorly studied and may harbour many unknown and, perhaps, already threatened species. One of these species is *Pseudolucia parana* Bálint, 1993, the sole representative of the large cosmopolitan subtribe Polyommatina in Brazil (VILA *et al.* 2011).

In 1902, on the basis of an unstated number of specimens, a small brown to light grey shiny (in fresh specimens) polyommataine butterfly was described from “Castro, Parana” and named *Lycaena griqua* Schaus, 1902. Since the description, practically no new information on the species appeared in the literature, although it was occasionally collected, and specimens were kept in the collection of Federal University of Paraná (Curitiba, O. Mielke, *pers. comm.*). In 1992 Zsolt Bálint, while working in the butterfly collection of the British Museum (Natural History) in London (now Natural History Museum, UK), checked a series of 14 male and 2 female specimens of a brown Brazilian lycaenid, identified as *L. griqua*. The name turned to be a homonym of *L. griqua* Trimen, 1887. The species looked similar to the widespread austral South American *Pseudolucia chilensis* (Blanchard, 1852). Specimens were dissected, and it was verified that *L. griqua* *sensu* SCHAUS (1902) indeed belongs to the genus *Pseudolucia* Nabokov, 1945 and, therefore, the new name *Pseudolucia parana* was proposed

(BÁLINT 1993). Subsequently it was found that *P. parana* forms a clade with two other species within the genus *Pseudolucia* (BÁLINT *et al.* 2000, BÁLINT & BENYAMINI 2001) and diverged early from the sister *P. chilensis* (GUERRA SERRUDO *et al.* 2018; see also later in this paper).

On 31st of December 2007 the type locality (“Castro, Paraná”; GPS 24°47’28”S, 50°00’26”W; elevation 997 m) was visited by one of the authors (DB). The site is located in a plateau of grasslands with scattered trees of the Paraná pine (*Araucaria angustifolia*) called “Campos Gerais”. It was inhabited by fifty immigrant Dutch families who turned Castro into a large modern agricultural farm called “Castrolanda”. This agro-industrial cooperative produces corn and soybean. Knowing that *P. chilensis* uses Dodders (*Cuscuta* spp., Cuscutaceae) as host plants (BENYAMINI 1995), an unsuccessful search for these parasitic plants was performed on the “islands” of natural vegetation within the boundaries of Castro. The natural reserve “Canyon Guartela” was also patrolled some 42 km NW of Castro with the same results; during three days in Castro no *Cuscuta* and no *P. parana* were found.

Looking for additional possible habitats for *P. parana*, DB corresponded with Olaf Mielke, who informed him that there were some specimens of *P. parana* in the collection at Universidade Federal do Paraná, Curitiba. On 19th of April 2010 the university was visited and 33 specimens of *P. parana* were located, collected between 1948 and 1986. Most of the specimens (n=17) originated from Guarapuava, Paraná (1200 m). As a consequence of urban development this habitat was completely destroyed and in recent visits by O. Mielke and one of his students in 2016, no butterfly was recorded. The second largest group of specimens (n=8) was collected by Mielke, between 1971–1981 in the geological state park Vila Velha, near Ponta Grossa. The last *P. parana* record originated from this site was a single male specimen collected by Andrew Warren in 2004.

On 20–21st April 2010 a two-day visit to the reserve located in the “Campos Gerais do Paraná” was carried out by DB, and AM accompanied by O. Mielke. Many localities were searched within this beautiful reserve, but neither *Cuscuta* nor *P. parana* were observed. Actually, out of the five polyommata that fly in Paraná – *Hemiargus hanno* (Stoll, 1790), *Leptotes cassius* (Cramer, 1775), *Zizula zyna* (W. H. Edwards, 1881), *Elkalyce cogina* (Schaus, 1902) and *P. parana* – only a few specimens of the first two common and migrant species were observed. In the collection of the Federal University of Paraná there are three *P. parana* specimens collected on 28th of February 1973 by O. Mielke at Vacaria (950 m) municipality. This city is located in the northern part of Rio Grande do Sul State, not far from the border with Santa Catarina State, a region with altitudinal grasslands. During various field trips in the region carried out earlier by AM and recently in 2015 by HPR, NOM and colleagues, no *P. parana* was found, apparently because almost all natural grasslands were converted into soybean monocultures.

News that *P. parana* was likely observed in mid-December 2008 on Morro Santana, in Porto Alegre (by Cristiano Iserhard, Federal University of Paraná,

UFP, *pers. comm.*; the first local record of *P. parana* population was observed by Daniel de Castro, a graduate student at PPG Biologia Animal – Federal University of Rio Grande do Sul) suggested that a population of this rare lycaenid could still exist there. This was the trigger to organise and launch expeditions to rediscover it, learn more about its biology and find the way to protect it and avoid its extinction. During the 7th International Conference on the Biology of Butterflies held between 11–14th of August 2014 in Turku, Finland, the authors DB, HPR and NOM agreed that *P. parana* is an extremely interesting and important species of the Campos Sulinos butterfly fauna, but because of data deficiency it is impossible to properly conserve it and its habitats, as other *P. parana* sightings in Rio Grande do Sul are several decades old. Therefore, the authors decided to launch a series of rescue-search expeditions for this species.

Because sites of recordings of the species were all rock fields, mostly at altitudinal grasslands or hill tops, fields at the top of granitic hills (morros) at the Porto Alegre region fulfilled the requisites for being habitat for the species. The tops of these hills are mostly covered by grasslands, because, due to their rocky nature, the soil is very shallow, sometimes no more than 20 cm deep and cannot support tree growth. This area is in the contact zone of the Atlantic forest to the north and the Pampa to the south. Botanically the type of habitat is campos sulinos (= southern grasslands) interspersed with semi-deciduous Atlantic forest.

This paper reports the results obtained and presents the information about the expeditions, the localities visited and the observations regarding the life history of *P. parana*, with conclusions on ecology and conservation.

MATERIAL AND METHODS

Specimens – The identification of *Pseudolucia parana* by the diagnostic traits (*cf.* BÁLINT & BENYAMINI 2001) is straightforward. Therefore *P. parana* material in collections is generally properly identified. This was the case in the visited collections: Federal University of Paraná (Curitiba, Paraná, Brazil) (UFP), Federal University of Rio Grande do Sul (Porto Alegre, Rio Grande do Sul, Brazil) (UFRGS), McGuire Center for Lepidoptera & Biodiversity (Gainesville, Florida, USA), Natural History Museum (London, UK) and National Museum of Natural History, Smithsonian Institution (Washington DC, USA). Data of the UFP specimens examined are given in Table 1.

With the field expertise of the authors it was also easy to locate and identify *P. parana* individuals in the visited locations. The supposed larval host plant (*Cuscuta* sp.) is also easy to identify because of its peculiar phenotype and parasitic life history. Plants were identified by consulting SETUBAL *et al.* (2011).

Vouchers of plants and insects (butterflies, ants) were collected by hand and prepared applying traditional methods. Samples were deposited in UFRGS.

Sites and observations – On the basis of information provided by museum specimens and anecdotal evidences we concentrated our effort in the state

Rio Grande do Sul, supplemented by a cross-country transect in Uruguay. During our visits to the localities, specimens, early stages, plants, and habitats were recorded with digital cameras, and observations were inscribed as field notes.

Molecular analyses – Molecular analyses were carried out in the Butterfly Diversity and Evolution Lab of the Institute de Biologia Evolutiva (CSIC-Universitat Pompeu Fabra), Barcelona, Spain. Legs were taken from recently collected individuals and the mitochondrial marker cytochrome c oxidase subunit I (COI) was amplified and sequenced following the method described in detail by TALAVERA *et al.* (2013) and by VODĀ *et al.* (2015). All new sequences of *P. parana* have been deposited in GenBank (accession numbers MN688540-MN688542). DNA barcoding sequences available in GenBank and BOLD for taxa within the *P. chilensis* species group were also used. A neighbour-joining phylogenetic tree was obtained using a HKY distance model in GENEIOUS PRO 6.0.5 with 100 bootstrap pseudoreplicates to assess the robustness of the tree clades.

Table 1. *Pseudolucia parana* records in the butterfly collection at the Federal University of Paraná, Curitiba (state Paraná, Brazil)

Locality, altitude, date, collector	wingspan (mm)	
	male	female
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	16.5	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	17	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	17	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	17	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	17.5	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	18	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	18	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	18	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	18.5	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	18.5	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	18.5	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	19	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider	19.5	
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider		17
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider		19
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider		19.5
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider		19.5
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Mielke & Schneider		20
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Schneider	18	

Locality, altitude, date, collector	wingspan (mm)	
	male	female
Guarapuava, 1200m, Paraná, 28.I.1972, leg. Schneider	18	
Guarapuava, 1200m, Paraná, II.1972, leg. Schneider		17
Guarapuava, 1200m, Paraná, II.1972, leg. Schneider		22
Ponta Grossa Campo, 900m, Paraná, IV.1951, leg. Felipe Justas	19.5	
Ponta Grossa Campo, 900m, Paraná, III.1948, leg. Felipe Justas	19	
Jaguariaiva Park, 1000m, Paraná, 6.II.1986, leg. Mielke & Casagrande	17	
Vila Velha N.P., 900m, Paraná, 4.IV.1981, leg. Mielke	16.5	
Vila Velha N.P., 900m, Paraná, 7.III.1973, leg. Mielke	20	
Vila Velha N.P., 900m, Paraná, 7.III.1973, leg. Mielke	18	
Vila Velha N.P., 900m, Paraná, 8.III.1971, leg. Mielke	17	
Vila Velha N.P., 900m, Paraná, 4.IV.1981, leg. Mielke	17	
Vila Velha N.P., 900m, Paraná, 6.II.1968, leg. Mielke		17
Vila Velha N.P., 900m, Paraná, 16.III.1972, leg. Mielke		17.5
Vila Velha N.P., 900m, Paraná, 7.III.1973, leg. Mielke		16
Vacaria, 950m, Rio Grande do Sul, 28.II.1973, leg. Mielke	17	
Vacaria, 950m, Rio Grande do Sul, 28.II.1973, leg. Mielke	18	
Vacaria, 950m, Rio Grande do Sul, 28.II.1973, leg. Mielke	18	
Average	17.92	18.45

FIELDWORK

Expedition 1

Location: Morro São Pedro (GPS reading for the location is: 30.18164°S, 051.11183°W; elevation: 110–130 m). Date: 14.XII.2014. Participants: DB, NOM, HPR & AM.

The site is a private property, situated 17.7 km SE of Porto Alegre centre. It is closed to visitors, permanently guarded, and in good ecological condition. On the day of the visit it was opened exclusively to the first “rescue” expedition.

At an elevation of 110–130 m, the forest opens to a grassland (“pampa”). Here the soil cover over the rocks is too thin for supporting trees (Fig. 1). *Cuscuta* was present by scattered singleton individual specimens. The first *P. parana*, a male, was observed at 12:30 (by HPR) nectaring on a violet flower of *Chrysolaena flexuosa* (Asteraceae). A female was observed flying from one *Cuscuta* to another, suggesting that these plants were the hosts, but we did not succeed to observe oviposition. In this habitat we recorded during ca. 40 minutes five adults, usually

flying about 50 cm above the ground, maneuvering low in the grass and landing on blades. We proceeded upwards crossing a small forest and at 13:30 arrived to the top. Here at 205 m a.s.l. (GPS reading: 30.17536°S, 051.11343°W) we found an excellent habitat where most of the suspected host plant and individual butterflies were observed. It was a shallow depression about 70 m in diameter, near the top of the hill, encircled by forest from one side and protected from the prevailing NW wind, typical in Porto Alegre during the summer. *Cuscuta* were quite common climbing on grasses, *Eryngium* sp., *Rhynchosia corylifolia* (Fabaceae) and other plants (Fig. 11). We stayed in this habitat until 16:00 and observed in total up to 20 butterflies. Males landed on grasses, *Eryngium* and the *Cuscuta* host plant – opening their wings in 90 degrees and oscillating their hindwings one opposite the other. A female was observed with closed wings walking low in the vegetation, possibly looking for *Cuscuta*. The adults were in worn to perfect condition reflecting an active breeding population, possibly with several overlapping broods or a long flight period.

Some *Cuscuta* branches with flowers were taken to be closely checked for early stages in the laboratories. Five mm long, small black ants that were wandering on the *Cuscuta*, likely to be hosts for the suspected myrmecophilous *P. parana* larvae, were taken for identification at UFRGS.

Expedition 2

Location: Morro Santana (GPS reading for the centre of the habitat is 30.06046°S, 051.12238°W; elevation: 284 m). Date: 15.XII.2015. Participants: DB, NOM, HPR & AM.

The site is adjacent to the UFRGS campus, within the urban boundaries of the city of Porto Alegre, 7.9 km from city centre and amidst growing unorganized human settlements. It is intended to be a preservation area and belongs to the university; however, so far, no practical action towards this end has been taken.

At 11:30 the hilltop was reached at 284 m a.s.l. and, soon after, the first (territorial) male was observed on the narrow track (DB). Until 15:30 several open areas up to the top of the hill were searched, but *P. parana* and *Cuscuta* were confined to the SW slope from 284 to 295 m a.s.l. A permanent western cool wind delimited the butterfly activity and most of the ca. 15 observed specimens were flying low near the host plants.

Summarising the visit to Morro Santana: the habitat of *P. parana* is much smaller than in Morro São Pedro and the number of observed *P. parana* was lower too. Here *Cuscuta* stocks are fewer and scattered. Though legally it is an “area de proteção permanente” (permanent protection area), this location shows obvious signs of human disturbance (fire, trampling, destruction of natural vegetation, erosion, etc.) and is susceptible to illegal occupation. It is definitely in urgent need of protection measures to ensure its conservation.

Expedition 3

Location: Park Municipal Saint Hilaire, 14 km E of Porto Alegre (GPS reading of the place: 30.10193°S, 051.08771°W; elevation: 104 m). Date: 18.XII.2016. Participants: DB & NOM.

The site visited was an open and humid place surrounded by trees with high stocks of *Eryngium* sp. (Apiaceae), which had buds about to bloom. It was around 10:00 in the morning, warm and damp weather with temperate of 30°C. The first *P. parana* was detected (by DB) flying very low inside the vegetation. Small and delicate *Cuscuta* stems were detected climbing especially on long blades of Poaceae. At 11:15 a female was observed flying amongst the grasses, no more than 50 cm over the soil, that immediately found a *Cuscuta* plant. After landing she displayed typical polyommatine lycaenid female behaviour: walking on the *Cuscuta*, oscillating the hindwings, touching the plant with abdomen tip, and laid several eggs. The wings were kept closed during all the time and aligned with direction of sun rays, and staying perpendicular only for short periods. Between 11:15 and 11:37 this individual was followed in the habitat, photographed, and it was observed that the wings were never opened for more than 10 degrees.

Only two *P. parana* individuals were observed in the site (one male, one female). Altogether, in the whole habitat only a few *Cuscuta* were found, all of them within a circle of ~30 m. It seems that the habitat was unfavorable for *Cuscuta*, which explains the rarity of *P. parana* at the site. There were clearings in the forest, normally on the top of the hills. The area was dominated by grasses, *Eryngium* sp. and a local palm (*Butia* sp.; for their importance see SOSINSKI *et al.* 2019). Subsequently, Camilla Goldas, a student on pollination at the Ecology Department (UFRGS), also collected a specimen in the same location.

A visit to 50 km S of Porto Alegre

Location: Itapuã State Park (GPS reading of the place: 30.36833°S, 050.99777°W; elevation: 0–263 m). Date: III.2016. Participants: HPR & colleagues.

Students on a field course, supervised by HPR, incidentally collected a male specimen in “Trilha da Visao” (= trail of vision) in Itapuã State Park. The voucher is in the UFRGS collection and one leg was taken for molecular analysis. The Itapuã State Park is located in the south of the Itapuã District of the municipality of Viamão, Rio Grande do Sul, 57 km south of Porto Alegre. It is on a promontory bounded to the south and east by Patos Lagoon and to the west by Lake Guaíba. It preserves one of the last remnants of the original vegetation in the Porto Alegre metropolitan area.

A visit to Uruguay

Date: 11–17.XII.2018. Participants: DB & Ofir Tomer.

In the second and third weeks of December 2018 the first author (DB), accompanied by his assistant Ofir Tomer, visited Uruguay in a north-south transect along circa 300 km. Although YUNCKER (1923) found four *Cuscuta* species in Uruguay, the chances to discover the species in the country were low because one of the authors (NOM) already looked for the butterfly and its larval host plant along the southern border of Brazil, but failed to find them. DB and Ofir Tomer started in north Uruguay, not far from the southern border of Brazil. Based in Melo, they searched to the north, east and west of the city looking for *C. taimensis* aff. *C. racemosa*, the host plant of *P. chilensis* in Chile (FERREIRA *et al.* 2014) (Fig. 23). Then they travelled southward visiting known localities for *C. taimensis* at: Arroyo Fraile Muerto (Cerro Largo), Arroyo Avestruz Chico (Treinta y Tres) and Minas, Cerro Campanero (Lavalleja). Finally, they searched the southern coast of Uruguay from Montevideo to Cabo Polonio National Park looking for *Cuscuta platiloba* (GONZÁLEZ & PICASSO 2015). During a one-week search, they did not find any *Cuscuta* or *P. parana*. It is quite possible that their visit was too early in the season, and a later mid-January visit to Uruguay should finally bring the answer whether *P. parana* is present in Uruguay or not.

RESULTS

The biology of *Pseudolucia parana*

Host plant – DB presented the first host plant family tree for the genus *Pseudolucia*, where *P. chilensis* was the only feeder on the *Cuscuta* branch (BENYAMINI 1995: 32). But in a later publication two more species were added to this branch, including *P. parana* with a question mark (BENYAMINI 2013: 171). The expeditions to the granitic hills of Porto Alegre proved that the hypothesis was correct: *P. parana* is tightly associated to the parasitic genus *Cuscuta*.

The genus *Cuscuta* contains 145 accepted species worldwide (MABBERLEY 1997, ANONYMOUS 2013). Approximately 23 species are distributed in 16 states along most of eastern Brazil (LORENZI 1982, SIMÃO-BIANCHINI & FERREIRA 2013), but only two are known in Porto Alegre: *C. corniculata* and *C. xanthochortos*.

The larval host plant of *P. parana* in Porto Alegre was identified by Priscila Ferreira (Fundação Zoobotânica, Rio Grande do Sul) as *C. xanthochortos* (Fig. 11), but the other species is a potential host plant as well. *Cuscuta* species may be toxic (ADLER 2000, GHULE *et al.* 2011), and implication of the toxicity on the female choice for oviposition is discussed in brief later in this paper. The presence of *C. xanthochortos* is also noted in the plant database Flora Digital do Rio Grande do Sul & Santa Catarina (ANONYMOUS 2019). According to this database, the flowering periods of this plant are December and February.

We believe that the activity of *P. parana* must be synchronised with the flowering periods of the plant, i.e. when the plant has buds, flowers and fruits to feed the larvae.

Egg – Several *Cuscuta* flowering heads, close to which females were flying, were collected from the visited morros for further inspection. In the laboratory eleven eggs were found; seven (63.7%) were laid on the host plant's filiform stems, three (27.3%) were laid on leaves and one (9.1%) on a flower bud. The egg is typical for a lycaenid (MUNGUIRA *et al.* 2015): flat, bagel-like, 0.5–0.6 mm in diameter; its colour is white (*cf.* Fig. 2). Several empty eggs were found, which suggests that the hatching first instar does not consume the eggshell.

Larva – On 15th of December 2014 in Morro Santana, close to the top of the *P. parana* SW slope habitat, at 295 m a.s.l., eggs and larvae were found on a host plant. First and second instar larvae were yellowish green. L3/L4 larvae were observed consuming *Cuscuta* flower buds, and were 7 mm long, yellowish, light green with narrow middorsal brown line with yellow margins and faint subdorsal oblique darker green strips. There were no hairs, dorsal nectary organ was observed, and the head was glossy. The fully grown L5 larva was up to 10 mm long, smooth, hairless, with cryptic colouration: light green with yellow lines similar to the yellow filiform stems and the white-yellow flowers of *Cuscuta*. In lateral view, the bolded top segment folds look like saw teeth (Fig. 3). A narrow broken brown dorsal line with yellow borders widened cephalad, subdorsal oblique faint green and yellow dashes and a yellow line around the periphery of the larva (Fig. 4). The head is glossy black.

Pupa – Two brown, smooth pupae were observed at the bottom of the breeding cage under *Cuscuta* stems. Both were horizontal, 6–7.2 mm long (7.5 mm in *P. chilensis*), no thoracic girdle was observed (exists in *P. chilensis*) (Fig. 5). One of them hatched after 5–7 days and a second brood specimen emerged (Fig. 7).

Diapause – The species probably overwinters as mature larva, similarly to the rest of taxa in the genus *Pseudolucia* and particularly to *P. chilensis* (BENYAMINI 1995: 15 & photoplate XIII: 19).

Myrmecophily – The dorsal nectary organ was visible in the caterpillars as a small crossline on the dorsum of the 7th abdominal segment. Small black ants were wandering over most of the *Cuscuta* stems and even near resting adults (Fig. 9); they were identified provisionally as *Dorymyrmex* sp.

Larvae of other species on Cuscuta in the habitats of P. parana – At least four more Lepidoptera larvae were recorded feeding on the local Brazilian *Cuscuta* spp.

1. A still unidentified hairstreak (Theclinae, Eumaeini) (Fig. 6); possibly the rare *Gargina gnosis* (Hewitson, 1868), since an adult was collected nearby a sitting female on *Cuscuta* plant in Morro Santana. In comparison with the larvae of *P. parana*, this larva is slightly larger in the last instar, hairy (with yellow hairs all over its body), the subdorsal signs are triangles and the head is glossy light brownish orange.

2. Still unidentified hairstreak (Theclinae, Eumaeini); the larva developed on branched spines.
3. Still unidentified hairstreak (Theclinae, Eumaeini); larva with purple spots and green head.
4. A long and narrow moth larva with long hairs.

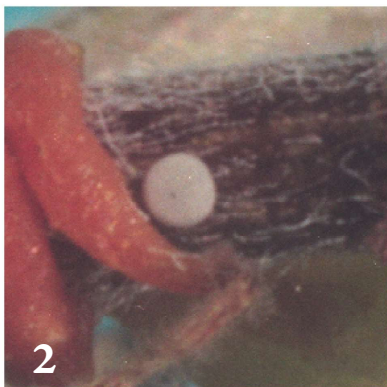
Ethology – Three territorial males were observed along 20 m of narrow trail at the top of Morro Santana's *P. parana* habitat. Typical air interceptions of two males included fast circling of one after the other for about five seconds at ca. 20 cm over the ground, and then they returned to their perch on the edge of low plants along the trail. After landing they opened the wings at 90 degrees and oscillated the hindwings (Fig. 10), which is a typical false head behaviour aiming to attract potential predators to the opposite side of the adult's head (SOURAKOV 2013, GALICIA *et al.* 2019). Some 30 m downwind of those territorial males, a motionless female was observed and photographed over a *Cuscuta* for several minutes, even allowing an ant to get close to it (Figs 8–9).

Adult nectar sources – In addition to the *Cuscuta* flowers, only few of the available flowering species were recorded as nectar sources for *P. parana*:

1. the most visited flowers were the yellow *Aspilia montevidensis* (Asteraceae);
2. the scattered purple *Chrysolaena flexuosa* (Asteraceae), which were in flower;
3. *Eryngium paniculatum* (Apiaceae); this dominant plant had just begun to bloom; it could become dominant nectar source later in the flight season.

Predators and parasites – We found “U” and “V” marks on the wings of 20% of the collected specimens. This relatively high percentage suggests that *P. parana* is strongly preyed upon. The marks on the wing membranes were produced most probably by lizards or birds and were divided evenly in the rear margins of the hindwings and the outer margins of the forewings.

During our visit to Morro Santana we photographed a flower crab spider (Thomisidae sp., Araneae) feeding on a *P. parana* male on an *Aspilia montevidensis* flower. One of the collected larvae was infected by a tachinid fly (Tachinidae sp., Diptera).



Figs 1–7. Documentations for the biology of *Pseudolucia parana* Bálint, 1993: 1 = habitat of *P. parana* at Morro São Pedro, Rio Grande do Sul, Brazil, on 14.XII.2014, showing semi-deciduous Atlantic forest surrounding grasslands (“campos sulinos”) (30.18164°S, 051.11183°W); adults of *P. parana* were observed in the pampa; 2 = egg of *P. chilensis* (Blanchard, 1852), taken on 12.X.1995, at sea level in Constitucion, Maule, Chile, placed very near to *Cuscuta* filiform stem; the egg of *P. parana* is identical; 3 = lateral view of L5 caterpillar showing bolded top saw teeth segments, taken on 15.XII.2014, at 295 m a.s.l., in Morro Santana, Rio Grande do Sul, Brazil; 4 = dorsal view of L5 caterpillar showing a narrow broken brown line with yellow borders that becomes wider cephalad running along the dorsum, taken on 15.XII.2014, at 295 m a.s.l., in Morro Santana; 5 = lateral view of pupa reared in laboratory, taken on 13.I.2015; 6 = dorsal view of an eumaeine lycaenid caterpillar taken on 15.XII.2014, in Morro Santana; 7 = pupal case (left) and adult (right) hatched in laboratory, taken on 3.I.2015 (photos 1–4 and 6 by Dubi Benyamini; 5 and 7 by Alfred Moser)

Phylogeny based on molecular analysis

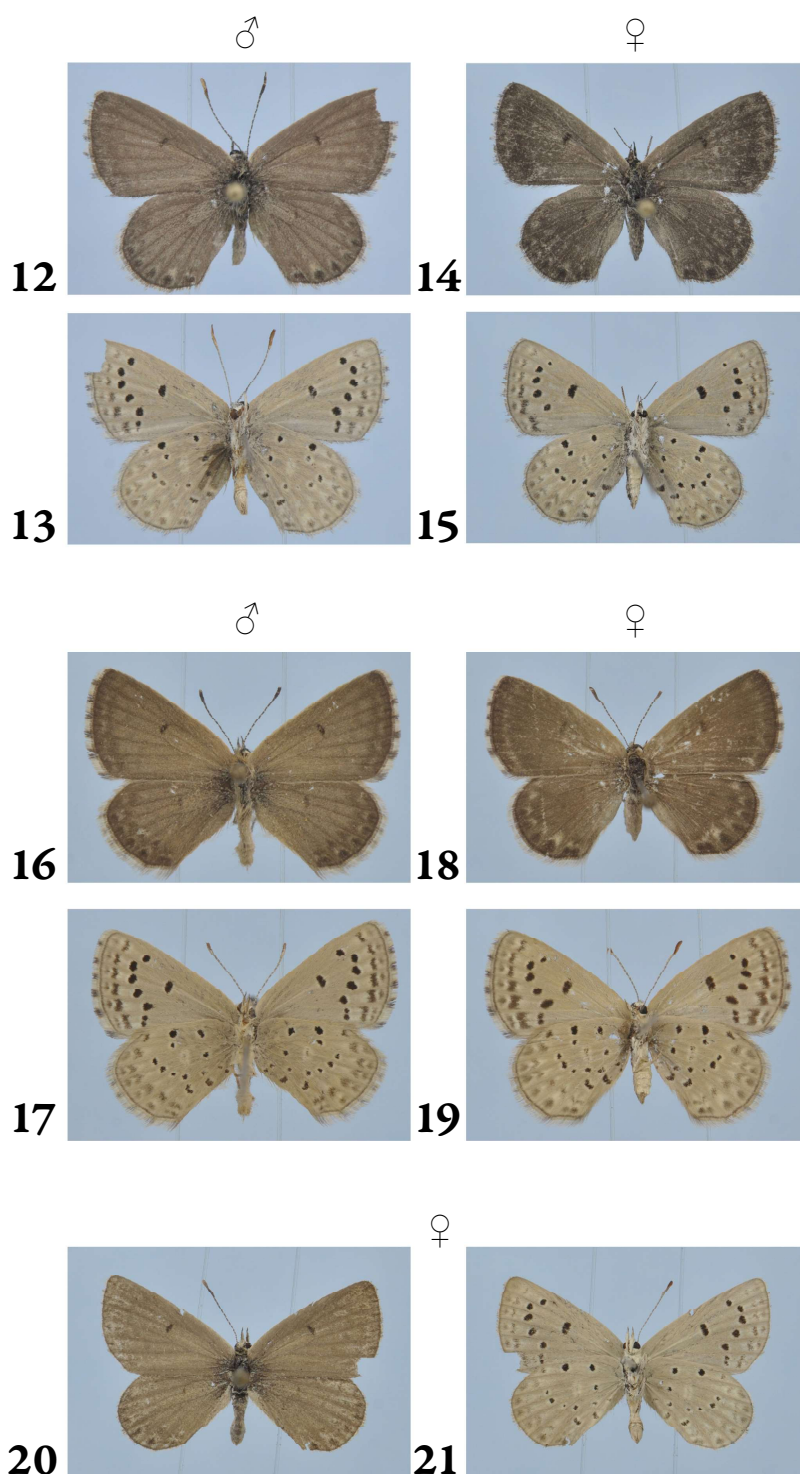
In the phylogenetic tree based on mitochondrial COI sequences (Fig. 22), the taxon *parana* is recovered as part of the *P. chilensis* species group and, in particular, as sister to the clade formed by *P. chilensis* + *P. sosneada* Benyamini et Bálint, 2015, with 100% bootstrap support and divergence (minimum uncorrected genetic distance) of 1.7%, which approximately translates to 0.7–1.1 million years, according to the generally accepted substitution rates for COI.

The recently discovered *P. “torotorensis”* (GUERRA SERRUDO *et al.* 2018) and the rediscovered *P. jujuyensis* Bálint, Johnson et Eisele, 2000 are sister taxa, with a 100% bootstrap support and diverged by 1.1% in COI. The minimum genetic distance between *P. “torotorensis”* + *P. jujuyensis*, to *P. parana* is 2.9%.

The last known population of Paraná (Villa Velha) is about 900 km north from the populations of Rio Grande do Sul (*cf.* Figs 12–21). Their minimum genetic distance is 0.3%, which suggests that they have been isolated since the last glaciation or even more (at least 12,000 years ago); however, note that only one specimen from Paraná was analysed.



Figs 8–11. Host plant documentation of *Pseudolucia parana* Bálint, 1993: 8 = a female searching suitable place to lay an egg, the wiggling *Cuscuta* is well visible close to her abdomen, taken on 18.XII.2016, in Parque Municipal Saint Hilaire, 104 m, Rio Grande do Sul, Brazil; 9 = an ant worker (*Dorymyrmex* sp.?) near the ovipositing female, taken on 15.XII.2014, at 295 m a.s.l., in Morro Santana, Rio Grande do Sul, Brazil; 10 = perching male, taken on 15.XII.2014, in Morro Santana; 11 = larval host *Cuscuta globiflora*, taken on 14.XII.2014, in Morro San Pedro, 205 m, Rio Grande do Sul, Brazil (photos by Dubi Benyamini)



Figs 12–21. Museum specimens of *Pseudolucia parana* Bálint, 1993 from Brazil, under same magnification. The Rio Grande do Sul specimens have more delicate wing surface pattern compared to that of Paraná specimens: 12–13 = male and 14–15 = female (recto and verso) from Morro Santana, Rio Grande do Sul, 285 m, 15.XII.2014, leg. D. Benyamini; 16–17 = male and 18–19 = female (recto and verso) from Guarapuava, Paraná, 1000 m, 28.I.1972, leg. O. Mielke & Schneider (male) and from Ponta Grossa, Vila Velha, Paraná, 900 m, 7.III.1973, leg. O. Mielke (female); 20–21 = female (recto and verso) from Vacaria, Rio Grande do Sul, 950 m, 28.II.1973, leg. O. Mielke. Scale: forewing costa length of the Fig. 12 = 11 mm (photos by Dubi Benyamini)

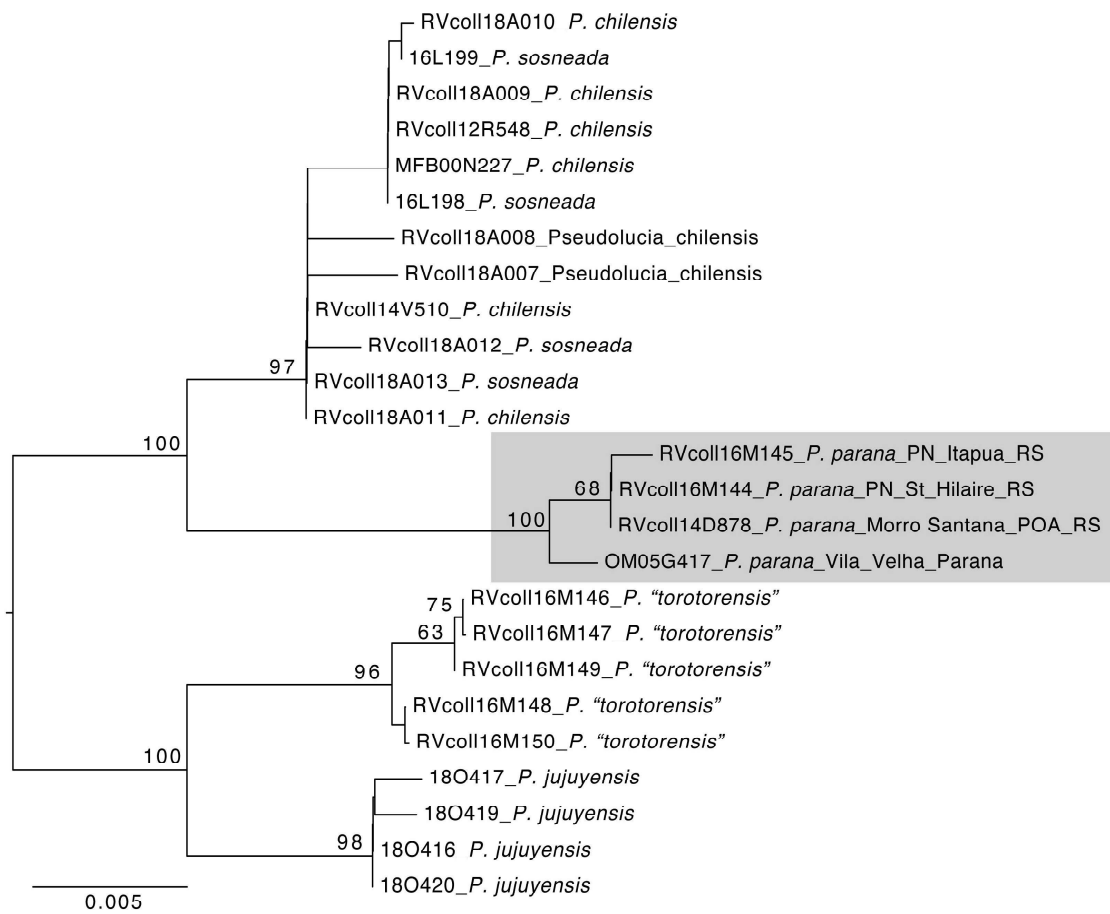


Fig. 22. Neighbour-joining tree based on the COI sequences for *Pseudolucia parana* Bálint, 1993 (highlighted), and its closest relatives. Bootstrap support values >50 are indicated. Scale represents 0.005 substitutions per site



Fig. 23. Distribution of *Cuscuta taimensis* in southern Brazil and eastern Uruguay (redrawn on the basis of FERREIRA *et al.* 2014)

DISCUSSION

The toxicity of *Cuscuta* and possible implications of the larval diet

Species of *Cuscuta* seem to be particularly prone to accumulate alkaloids from a variety of host plants and, for example, the toxic glucoside trehalose has been detected in *C. reflexa* (CZYGAN *et al.* 1988, WAGSTAFF 2008, BURROWS & TYRE 2012). BENYAMINI (1995: 45–48 & Fig. G) placed *P. chilensis* female with its reddish brown warning colouration in the centre of a large Chilean mimicry ring. While the larvae consume toxic *Cuscuta*, other reddish-brown mimics consumed other toxic plants, i.e. all members of the *P. andina* species group consume host plants of the genus *Astragalus*, known as addictive to livestock and called in Spanish “Yerba Loca” (the crazy plant). So, why did *P. parana* not develop warning colours that could serve as protection against predators? The same question applies to the two other species of the *P. chilensis* species group: (1) *P. jujuyensis* Bálint, Johnson et Eisele, 2000 (no orange markings) (BÁLINT *et al.* 2000) and (2) *P. sosneada* (which has minimal orange markings on the female’s upper forewings) (BENYAMINI & BÁLINT 2015).

A potential hypothesis is that some species of *Cuscuta* are less toxic than others, or that toxicity depends on which plant the *Cuscuta* is parasitizing. However, differences in the communities of predators might also be an explanation.

Classification and taxonomy of *Pseudolucia parana* based on traditional and molecular characters

P. parana belongs to the *P. chilensis* species group of *Pseudolucia*, which is characterized by the following adult morphological traits: (1) dorsal wing surfaces of both sexes are coloured with brown pigments, without sexual dimorphism typical of the genus; (2) the pattern of the ventral wing surface is typical polyommataine (with spots), grossly contrasting most of the other members of the genus (with arrow-head marks) (*cf.* NABOKOV 1945); (3) aedeagus extremely stout and the suprazonal portion is very short and pointed; (4) the long and membranous female ductus is heavily folded. All these characters were considered to be plesiomorphic, suggesting a basal position of the species group in the phylogeny of the genus (NABOKOV 1945, BÁLINT & BENYAMINI 2001).

Previous molecular analyses (VILA *et al.* 2011, GUERRA SERRUDO *et al.* 2018) confirmed this hypothesis: the *P. chilensis* species group was monophyletic and sister to the rest of the genus. In the phylogenetic tree based on mitochondrial COI sequences here presented (Fig. 22), the taxon *P. parana* is recovered as part of the *P. chilensis* species group and, in particular, as sister to the clade formed by

P. chilensis + *P. sosneada*. Based on the tree divergences, we can estimate an age for *P. parana* of approximately 1M year old.

Further division apparently happened during the last glaciation or even before, when Porto Alegre and Paraná populations were split. The two stocks seem to be genetically and morphologically slightly distinct (Figs 12–19), but a single specimen from Paraná was sequenced and further evidence has to be collected to support their taxonomic distinction.

The proposed phylogeny of *P. parana* underlines the importance of the granitic hills of Porto Alegre region: they provide the last refuges for relict taxa that evolved under conditions very different from the current situation (SETUBAL *et al.* 2011).

Distribution, human influence, sampling

Butterfly distribution analyses often suffer serious data deficiency and available records frequently show the activity of lepidopterists rather than the actual distribution of the species. In the case of *P. parana*, however, the following considerations underline that the data available on the species reflect that the species is indeed rare, very specialised and habitat specific. The intensive lepidopterological investigation in Brazil started in the 19th century, and the Southern Region (states Paraná, Santa Catharina and Rio Grande do Sul) were some of the most intensively sampled ones. Because of the large number of European immigrants and climate similarities to their original home, “Nova Teutônia” in southern Brazil offered better conditions and logistics compared with other areas of those times, resulting an intensive butterfly trade and earlier lepidopterofauna surveys than in other parts of South America. However, classical workers, like Fritz Müller (1821–1897), Adolpho Pompilio P. Mabilde (1850–1892), Hans Fruhstorfer (1866–1922), Czesław Marian Bieżanko (1895–1986) and Fritz Plaumann (1902–1994) were all keen to explore and describe the biodiversity of the region, including the smallest butterflies, such as *P. parana*, but they did not collect the species. More recently, i.e. at least in the last three or four decades, quite a few entomologists worked intensively on the butterflies of southern Brazil (see, e.g. CORSEUIL *et al.* 2004, DOLIBAINA *et al.* 2011, MIELKE 1995, MORAIS *et al.* 2007, PAZ *et al.* 2013, SIEWERT *et al.* 2014, TESTON & CORSEUIL 2008, and references therein), including three of us (NOM, HPR and AM).

Therefore, we suggest that the species is indeed very rare. In the early period of lepidopterology, samples were available only for Schaus, who described the taxon. This rarity can be confirmed by the observation that historical samples of *P. parana* can be found only in the Natural History Museum (London, UK), which contains a portion of Dukinfield E. Jones’ collection via the Rothschild Bequest (BÁLINT 1993). Jones collected the *Lycaena griqua* type material preserved in the Smithsonian Institution, and also in the McGuire Center (Gainesville, Florida, USA).

The data for Paraná State where "*Lycaena griqua*" was discovered obviously testify that the morro habitats are under considerable threat, as at the turn of the 20th–21st centuries the land use in Paraná state has become more intensive to a manner that destroys the ecosystem. In spite of intensive search in the second decade of the 20th century, the species could not be found in the localities of Castro, Guarapuava, Jaguariaiva, Ponta Grossa Campo and Vila Velha. DOLIBAINA *et al.* (2011) report that natural fields were present until the mid-1970s in the Guarapuava region, where the last records for *P. parana* originate (see Table 1); then the remnants were increasingly replaced by monocultures. In 2011, only three small patches under five hectares were left, two of which have now disappeared. The lepidopterofauna of this phytophysionomy is critically under threat, as no protected area provides such vegetation in that state; *P. parana* is most probably extinct there.

In Rio Grande do Sul the current situation is not much better: grassland physiognomies are hardly ever included in preserved areas, and almost always these areas are surrounded by huge expanses of environmental matrix unfavorable for butterfly dispersal. It is symptomatic that all four locations where *P. parana* was found are within parks. However, in addition to the actual fields where they were found are very small, the level of implementation and protection is satisfactory in only one of these (Itapuã State Park).

In 2014, *P. parana* was included in the red list of endangered species of the state of Rio Grande do Sul in the category Endangered (EN; B1ab (iii)) (Decree No. 51.797, of 8 September 2014), given the very few published records for the species, although researchers have been working in their region in the last decade. Its global extent was restricted ($\sim 4000 \text{ km}^2$), its natural habitats – the native rock and altitude fields – being under increasing anthropogenic pressure and threatened with fragmentation and destruction by various types of activity: agriculture, livestock, fire, forestry, urbanization and even climate change.

Recently, the status of *P. parana* was reassessed in a workshop for definition of priority areas in the Pampa for conservation and it was strongly recommended that its status should be changed to critically endangered (CR B2b(iii)): currently, in addition to the very few records described above, this endemic grassland species is restricted to the granitic hills of Porto Alegre, and by ecological niche modeling and satellite habitat assessment, its whole area of occupancy is estimated to be smaller than 3.5 km^2). Although this species is listed as not evaluated globally by the IUCN, given that it is a Brazilian endemic that has not been documented outside the states of Paraná and Rio Grande do Sul, the data here provided indicate a global status of Critically Endangered for *P. parana*.

P. parana is an important species because it indicates the unique ecosystem confined to the top of these granitic hills at this southernmost region (Fig. 24). Consequently, it could be considered as a flagship species for the conservation of these habitats. Only recently has the butterfly fauna of Campos Sulinos been in the focus of studies. Data has grown a lot in the last ten years, but much information

is still lacking. Given the speed at which native fields are being altered, protective actions are essential, as there is a real risk that other species will become extinct without even being documented. There is already strong evidence of extinct species in the natural fields in regions of south Brazil, given the nearly complete destruction or degradation of these habitats. Some species, however, such as *P. parana*, can still be found as small remnants, in need of urgent conservation effort. Many other species in similar situations might exist. The best strategy for their conservation is more thorough research on their biology and ecology, and to make the conservation and restoration of their natural habitats a priority.

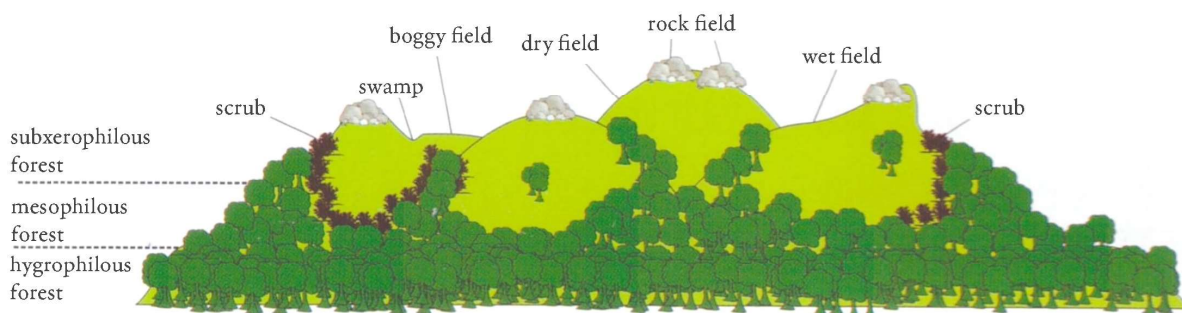


Fig. 24. Altitudinal gradient schematic profile and position of rural and forest communities along the top of a hill ("morro") in Porto Alegre, Brazil. The habitats of *Pseudolucia parana* are on the top region where rock fields are situated (based on SETUBAL *et al.* 2011)

*

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